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CONIFER TREE DISTRIBUTIONS IN SOUTHERN CALIFORNIA

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ABSTRACT

Maps and text describe current distributions of 19 conifer tree species in southern California. Distributions are related to climate, geology, terrain, and other aspects of the environment. Corrections to earlier published descriptions and maps are highlighted. Although species are discussed as components of six vegetation types (closed-cone conifer forest, foothill woodland, mixed evergreen forest, pinyon-juniper woodland, mixed-conifer forest, and subalpine forest), the distribution maps are for species, not vegetation. Species limits correspond to a density as low as 1 tree of the species of concern per 10 ha. Some changes in distribution over the past century, primarily due to fire, can best be interpreted and understood when a species is placed correctly in one of three models: shifting populations, standing populations, and patch mosaic populations.

Because of their value for lumber and fuelwood, the distribution of coniferous trees in southern California has been described since Europeans first settled the region in the late 18th century (Minnich 1988; Minnich and Franco-Vizcaíno 1998). Early accounts include descriptions in Spanish diaries, the Pacific Railroad Survey of the 1850s, the US–Mexico Boundary survey of 1894, early explorers, and reports of the U.S. Forest Service. The first maps published over 100 years ago by Kinney, Grinnell, and in Forest Reserve Reports were impressionistic or based on life zone theory (Minnich 1988). While forest distributions were realistic, boundary criteria were not explicitly defined. The first objective maps were produced by the Vegetation Type Map Survey (VTM) in 1929–34 (Colwell 1988) on the basis of physiognomy and dominance criteria. Map accuracy was compromised because boundaries were drawn in the field without the advantage of aerial photographs, and their precision was reduced by planometric error of triangulated 1900 topographic base maps. Still, the VTM maps show high quality and are consistent with the earliest aerial photographs in 1928–1939. Griffin and Critchfield (1976) reproduced the ranges of California trees based largely on maps of the VTM survey.

The population size and extent of species of course are dynamic, so it is essential to update maps to ascertain the impacts of natural disturbances and land management. Using aerial photographs, this study produces maps of coniferous trees in southern California south of lat. 35° and west of the Mojave and Colorado Deserts. In southern California's mediterranean climate, wildland fire is strongly integrated into the ecological function of conifer species. Because conifers are largely nonsprouters, stand-replacement fires have produced important changes in species ranges since the VTM survey. The objectives of this study are to produce a modern baseline of distributions for comparison with the VTM survey, to correct taxonomic errors of the VTM survey, describe species ranges in relation to climate, geology, terrain, and other aspects of the environment, and to evaluate species changes over the 20th century.

Among the various reasons for conducting the VTM Survey, Wieslander (1935) stated that it was important to produce a baseline of vegetation for purposes of replication at some time in the future. Likewise, the hope of this survey of southern California conifer forests is to encourage resurveys to evaluate their broad-scale dynamics over long time scales.

Coastal Southern California. Most conifers grow in the Transverse and Peninsular Ranges that divide the Mojave and Sonoran Deserts from the coastal plains and valleys (Fig. 1). The Transverse Ranges extend from Point Conception to Joshua Tree National Park. The Santa Ynez Mountains join the San Rafael and Sierra Madre Mountains of the South Coast Range of central California. From this junction, a series of parallel ridges that include the Ortega, Santa Paula, and Topatopa Mountains, and Pine Mountain Ridge merge into a single chain that includes the Liebre, San Gabriel, and San Bernardino Mountains, and the plateau of Joshua Tree National Park (place names are located in Table 1). The Tehachapi Mountains of the Sierra Nevada terminate at the Lockwood Valley plateau that contains isolated undissected ranges, including Frazier Mountain, Alamo Mountain, and Mt. Pinos. The plateau is bordered on the north by the San Emigdio Mountains. The north-south Peninsular Ranges include the San Jacinto Mountains that extend from San Gorgonio Pass to the Santa Rosa Mountains. To the west is a series of coastal ranges including the Santa Ana, Palomar, Volcan, Cuyamaca, and Laguna Mountains. Elevations in Transverse Ranges frequently exceed 2000 m, and reach 3080 m at Mt. San Antonio and 3499 m at Mt. San Gorgonio. The more subdued Peninsular Ranges are typically 1000–1800 m, although summit altitudes reach 3273 m at Mt. San Jacinto.

Table 1. Location of Place Names Used in Text.

Place name	Latitude (°N)	Longitude (°W)
Aguanga	33 27	116 52
Alamo Mountain	34 40	118 56
Azusa	34 09	117 55
Banner Canyon	33 05	116 33
Barton Flats	34 10	116 53
Bautista Canyon	33 40	116 47
Beechers Bay, Santa Rosa Island	33 59	120 10
Big Bear	34 15	116 56
Big Pine Mountain	34 42	119 39
Big Tujunga Canyon	34 20	118 05
Bluff Lake	34 13	116 58
Butler Peak	34 16	117 00
Cattle Canyon	34 15	117 41
Cerro Nordeste	34 50	119 13
City Creek	34 07	117 10
Cobblestone Mountain	34 36	118 52
Coxcomb Mountains	34 02	115 20
Crestline	34 15	117 15
Cucamonga Peak	34 14	117 35
Cuddy Valley	34 50	119 02
Cuyama River	34 45	119 20
Deep Creek	34 18	117 07
Doone Vallye	33 20	116 55
Eagle Mountains	33 49	115 40
Figueroa Mountain	34 45	119 57
Frazier Mountain	34 47	118 59
Garner Valley	33 37	117 40
Gavilon Hills	33 48	117 20
Government Peak	34 09	117 05
Grapevine Canyon	34 23	117 04
Guatay	32 51	116 34
Gypsum Canyon	33 50	117 43
Hagador Canyon	33 48	117 37
Hesperia	34 24	117 20
Holcomb Creek	34 18	117 00
Holcomb Valley	34 19	116 55
Hurricane Ridge	34 46	119 47
Icehouse Canyon	34 15	117 40
Idyllwild	33 45	116 43
Japacha Peak	32 56	116 43
Keller Peak	34 12	117 03
La Brea Creek	34 57	119 58
Lake Arrowhead	34 15	117 11
Lake Hemet	33 40	116 42
Lake Mathews	33 51	117 26
Lake Piru	34 29	118 45
Lakeview Mountains	33 46	117 04
Lazaro Canyon	34 49	119 50
La Rumerosa	32 30	116 03
Lockwood Valley	34 45	119 02
Los Pinos Mountain	32 46	116 36
Lytle Creek	34 14	117 27
Manzanita Creek	34 47	119 54
McCain Valley	32 45	116 20
Mill Creek	34 05	116 56
Mt. Baden-Powell	34 22	117 46
Mt. Grinnell	34 07	116 49
Mt. Laguna	32 52	116 25
Mt. San Antonio	34 17	117 39
Mt. Waterman	34 21	117 56
Mt. Wilson	34 13	118 04
Ojai	34 27	119 15
Ontario Peak	34 14	117 38
Onyx Summit	34 11	116 43
Ortega Hill	34 34	119 23

TABLE 1. CONTINUED.

Place name	Latitude (°N)	Longitude (°W)
Otay Mountain	32 35	116 52
Palmdale	34 35	118 05
Palm Divide	33 42	116 39
Perris	33 48	117 14
Phelan	34 26	117 34
Pinyon Ridge	33 11	116 26
Pinyon Flat	33 37	116 27
Pine Valley	32 50	116 31
Pleasants Peak	33 47	117 38
Pleasant View Ridge	34 25	117 55
Plunge Creek	34 09	117 09
Prairie Fork	34 20	117 42
Purisima Hills	34 44	120 27
Rabbit Peak	33 26	116 14
Raywood Flat	34 03	116 50
Redlands	34 03	117 11
Riverside-Perris Plain	33 50	117 15
Rock Creek	34 25	117 50
Running Springs	34 13	117 06
San Bernardino Ridge	34 08	116 54
San Emigdio Mountains	34 50	119 00
San Gorgonio Mountain	34 06	116 50
San Rafael Mountain	34 43	119 48
Santa Paula Peak	34 26	119 00
Santa Susana Mountains	34 20	118 35
Sawmill Mountain	34 42	118 34
Sespe Creek	35 37	119 22
Sisquoc River	34 51	119 50
Soledad Canyon	34 27	118 18
Sugarloaf Mountain	34 12	116 51
Sulphur Spring Canyon	34 45	119 53
Tahquitz Peak	33 45	116 40
Tecate Peak	32 35	116 43
Temescale Canyon	33 46	117 30
Thomas Mountain	33 38	116 42
Throop Peak	34 21	117 48
Tip Top Mountain	34 15	116 42
Topatopa Mountains	34 32	119 00
Torrey Pines State Beach	32 57	117 16
Vandeventer Flat	33 33	116 33
Warm Springs Mountain	34 36	118 35
Waterman Canyon	34 12	117 17
Whale Peak	33 02	116 18
Wright Mountain	34 20	117 39
Wrightwood	34 21	117 39
Zaca Ridge	34 46	120 01

The climate is mediterranean with winter precipitation and summer drought. Mean winter temperatures range from 10°C in the coastal and desert areas to 0°C at 2500 m in the mountains. Mean temperatures in summer range from 38°C in the desert to 15°C at 2500 m. A shallow marine layer results in mean temperatures of 18–22°C at the coast increasing to 27°C in inland valleys.

Large differences in local conifer species zonation result from strong gradients in average annual precipitation (AAP, Fig. 2). Most precipitation occurs during cold fronts arriving from the North Pacific Ocean. Because winds aloft are southwest to southerly (Minnich 1984), physiographic lift is strongest on the south front of the Transverse Ranges, with the highest AAP in coastal escarpments of the "upwind" Topatopa, San Gabriel, and San Bernardino Mountains (AAP, 90–110 cm). Amounts decrease toward downwind ranges and watersheds—regardless of altitude—due to depletion of storm air mass moisture and descending airflow in rain shadows, including the San Rafael Mountains, Pine Mountain Ridge, Big Bear, and upper Santa Ana River (AAP, 60–80 cm). Farther inland, the San Emigdio, Tehachapi, and Liebre Mountains, Mt. Pinos, and lee slopes near Big Bear receive only 35–60 cm AAP. The AAP is only 40–60 cm in the Peninsular Ranges because slopes parallel

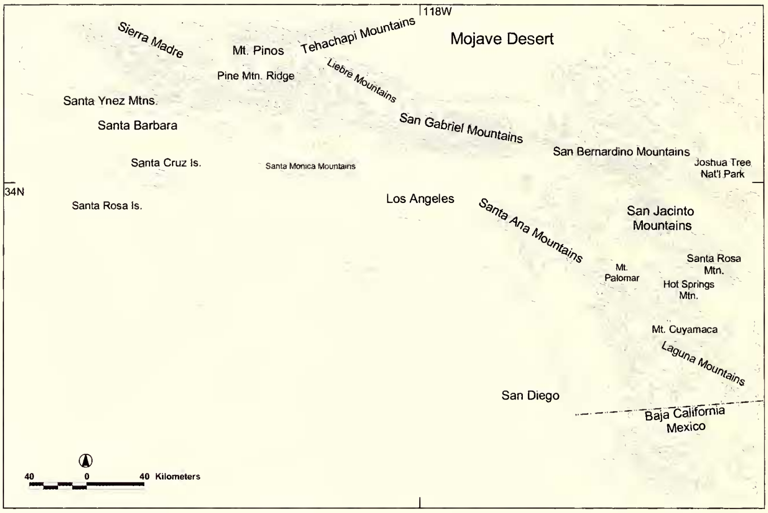

FIG. 1. Location map and place names in southern California. Topographic maps and elevations were developed from United States Geological Survey 1:250,000 Digital Elevation Models (USGS 2000).

storm winds. Amounts locally reach 80–100 cm on local southern escarpments of the Santa Ana Mountains, Mt. Palomar, and Cuyamaca Peak. The San Jacinto Mountains receive 40–70 cm and the Santa Rosa Mountains receive <50 cm because they are leeward of the Santa Ana and Palomar Mountains. The AAP decreases to 10–20 cm in the Mojave and Sonoran Deserts.

METHODS

The large size and distinct morphology of conifers permits accurate mapping to species level using aerial photographs. Maps were interpreted from aerial photographs using a roll film stereoscope (on file in the Department of Earth Sciences, University of California, Riverside). Trees were identified on the basis of their crown perimeter and apex configurations, vertical structure, shadows, and color. We field verified for tree occurrence in all southern California ranges. Procedures are summarized in Minnich (1987a) where maps of many of the same species in northern Baja California were presented.

Distributions were interpreted from a variety of aerial photograph coverages of the entire region taken mostly between 1971–1980 including the Mission 164 coverages of California and photographs taken in 1938–1939. Site-specific georeferencing of repeat aerial photographs on a Zoom Transfer Scope (ZTS) reveals that virtually the same mature trees can be matched on the earliest

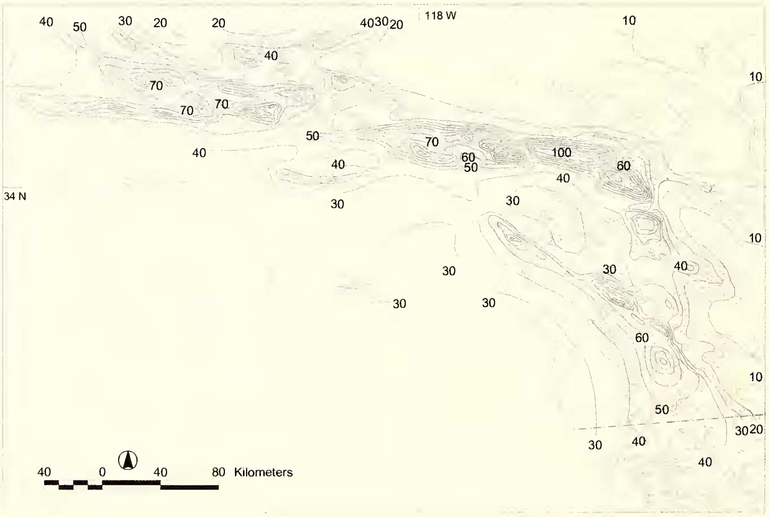

FIG. 2. Mean annual precipitation (after California 1980).

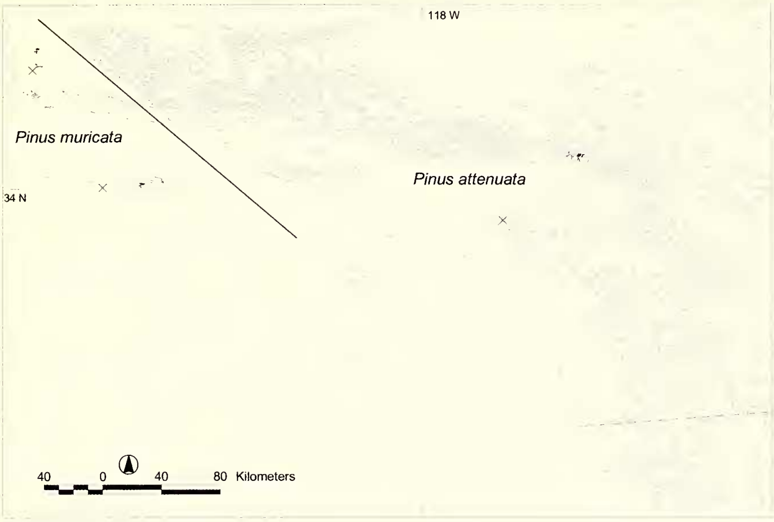

FIG. 3. The distribution of *Pinus attenuata* and *P. muricata.* Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

and most recent photograph coverages. However, rapid changes occurred in all species from stand-replacement burns. Recent flights (>1990) were examined for stand-replacement burns to update conifer species distributions since the Mission 164 flights.

Since the objective is to map broad species ranges, rather than forest dominance patterns, we defined the limit of species as a minimum threshold of one tree per 10 ha. This criterion allows for more detailed range maps than depicted from Griffin and Critchfield's definition of "group of stands more than two miles (3 km) across, or stands less than two miles (3 km) across or of unknown size." It also excludes rare outposts that would result in excessive detail. Botanical collections are included for the occurrence of outposts outside our species ranges.

Boundary data were georeferenced and transferred onto 1:250,000 scale topographic sheets (USGS 2000) using a ZTS. Contour creation using DTED Level 0 data (NIMA 2001) and subsequent spatial manipulations were performed by Geographical Information Systems using ESRI (2000) software. Graphic versions of the species maps are accessible from our website (http://spotfire/ucr.edu/socaltree). Changes in forest distributions can be evaluated by comparing website maps with published and unpublished VTM quadrangle maps under curation at the University of California, Santa Barbara.

DISTRIBUTIONS

Conifer tree ranges are presented under six vegetation types, as recognized in Barbour and Major (1988): closed-cone conifer forest, foothill woodland, mixed evergreen forest, pinyon-juniper woodland, mixed-conifer forest, and subalpine forest. Species ranges are given from northwest to southeast. Total stand area for each species was obtained from the GIS software. Most conifers grow elsewhere in California and western North America (Critchfield and Little 1966; Griffin and Critchfield 1976; Hickman 1993) and extend into northern Baja California (Minnich 1987a; Minnich and Franco-Vizcaíno 1998). Statements on substrate are based on the Southern California Areal Mapping Project (SCAMP 2000). Place names are given in Table 1.

Closed-cone conifer forest. Closed-cone conifer forest includes three taxonomic groups: serotinous pines in *Pinus* subsect. *oocarpae* (*Pinus attenuata* Lemmon, *P. muricata* D. Don; taxonomy and variation reviewed in Millar 1986), the partially serotinous *Pinus* sect. *sabinianae* (big-cone pines, *P. coulteri* D. Don and *P. torreyana* Carrière), and two cypresses, *Cupressus arizonica* E. Greene ssp. *arizonica* of the *C. arizonica* complex and *C. forbesii* Jepson (Rehfeldt 1997). *Pinus coulteri* and *P. torreyana* are treated here due their similar fire ecology to species in *Pinus* subsect. *oocarpae* (Haller 1986) and cypresses (Vogl et al. 1988). However, the big-cone pine *P. sabiniana* Douglas is treated as a member of foothill woodland. Closed-cone conifer forests grow in chaparral with stand-replacement fires resulting in spatially synchronized even-aged, short-lived stands. Distributions in southern California are fragmented, with stand boundaries frequently unrelated to local environmental gradients due apparently to stochastic recruitment failures after fire (Vogl et al. 1988). Nearly all closed-cone conifers are found in monospecific stands.

Pinus muricata D. Don (937 ha, Fig. 3).—Small, compact stands of bishop pine are found within 20

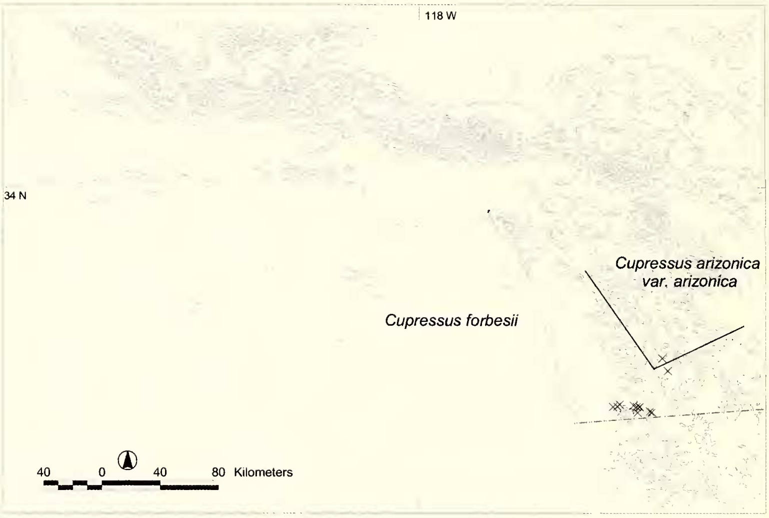

FIG. 4. The distribution of *Cupressus arizonica* var. *arizonica* and *C. forbseii.* Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

km of the Pacific Coast in the Purisima Hills and the west end of Santa Ynez Mountains. Offshore stands include two colonies on Santa Rosa Island and larger stands on Santa Cruz Island. Mainland stands grow on diatomaceous shales or Careaga sandstones, which produce shallow, highly acid soils with high water-holding capacity (Schoenherr 1992). Island stands grow on a variety of substrates (Vogl et al. 1988). While the AAP ranges from 35–55 cm, fog drip is important to the seasonal distribution of soil moisture (Vogl et al. 1988). Bishop pine grows between 200 and 400 m within the range of coastal low clouds in summer (DeMarrais et al. 1965). The concentration of stands on exposed ridgetops and western exposures optimize foliar fog condensation in strong northwesterly winds of the marine layer. Low temperatures reduce summer transpiration. Bishop pine has recently sustained heavy mortality from needle blight caused by *Dothistroma septospora* (Ades et al. 1992). Most stands on Santa Cruz Island have been degraded or extirpated by grazing and rooting of feral sheep and pigs since 1855 (Brumbaugh 1980; Minnich 1980). The designation of *P. remorata* Mason for trees on Santa Cruz Island has been merged with *P. muricata* (Millar 1986).

Pinus attenuata Lemmon (721 ha, Fig. 3).—Scattered even-aged stands occur in the San Bernardino Mountains from City Creek to Government Peak between 1000 and 1400 m. A VTM error showing a large stand on Keller Peak was a confusion for juvenile *P. coulteri* stands regenerating from fire about 1905 as seen in 1938 aerial photographs. Knobcone pine grows on concave summits and ridges of granitic substrate with thin chaparral dominated by *Adenostoma fasciculatum* Hook. & Arn., *Quercus wislizeni* A.DC., and *Arctostaphylos glandulosa* Eastw. (Minnich 1999). While almost all stands were burned in 1938, 1956, and 1970, there was abundant post-fire regeneration in the same areas. Two colonies grow in the Santa Ana Mountains at 1000 m: one on the west slope near Pleasants Peak (Vogl 1973), and the other 2 km NE in Hagador Canyon. Both grow on fine-grained, acidic soils associated with hydrothermally altered volcanics (Vogl et al. 1988). The AAP ranges from 50 to 80 cm. Supplemental soil moisture from fog drip is seasonally phased with wet soils from winter storms and may not reduce drought stress in summer. Coastal stratus at the elevations of *P. attenuata* is most frequent in late spring when fog drip totals reach 10 cm per month (Vogl 1973). The climate is warm and dry in summer because stands lie above the marine layer (normally <600 m, DeMarrais et al. 1965).

Cupressus forbesii Jepson (268 ha, Fig. 4).—This Baja California species grows on north-facing slopes between 200 and 1200 m at four localities: an isolated stand in Gypsum Canyon in the northern Santa Ana Mountains, and at Guatay, Tecate Peak, and Otay Mountain in San Diego Co. (AAP, 40–70 cm). Tecate cypress was reported from Hot Springs Mountain in 1880 (Griffin and Critchfield 1976). The Tecate Peak and Otay Mountain stands grow on alkaline clay soils derived from gabbro basalts rich in iron and magnesium (Zedler 1981; Schoenherr 1992). The stand at Guatay grows on granite. The Gypsum Canyon stand grows on Paleocene sandstone, where trees over 200 years old were recorded on canyon floors (Schoenherr 1992). It was not shown in Griffin and Critchfield (1976), although the stand was recorded on VTM quadrangle maps. Gene frequency data shows that genetic distance was not significantly associated with geographic distance between populations (Truesdale and McClenaghan 1998). Variable fire intervals

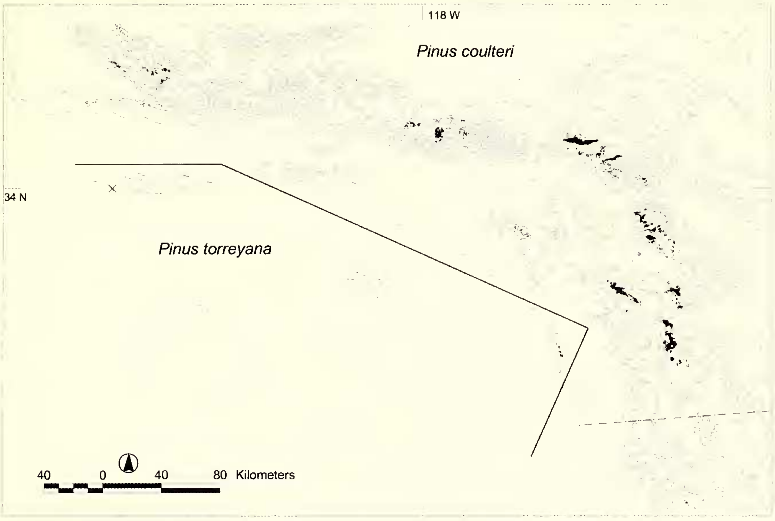

FIG. 5. The distribution of *Pinus coulteri* and *P. torreyana*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

over long-time scales encourage small-scale extinctions and reinvasions (Zedler 1981). Stand degradation may be rare because only 6.0% of the chaparral sustained fire intervals shorter than 20 years during 1920–1972 (Minnich and Chou 1997). The Gypsum Canyon stand regenerated well after a stand-replacement fire in 1948 (Griffin and Critchfield 1976). In northern Baja California, hundreds of even-aged groves grow in a fine-grained chaparral patch mosaic of numerous small burns (Minnich and Chou 1997).

Cupressus arizonica E. Greene *ssp. arizonica* Reyfeldt (5.3 ha, Fig. 4).—A single stand grows on a chaparral-covered west-facing slope of Mt. Cuyumaca near Japacha Peak at an altitude of 1400 m (AAP, 75 cm). Discriminant analysis of 15 genetic traits align the Cuyumaca cypress population in the *C. arizonica* spp. *arizonica* complex which occurs in Arizona and northwestern Mexico; the Cuyamaca population may also occur among inbred lines (Rehfeldt 1997). The nearest stand occurs in the southern Sierra Juárez of northern Baja California (Broder 1963). This tree was formerly classified as *C. stephensonii* C.B. Wolf and *C. arizonica* var. *stephensonii* (C. B. Wolf) Little.

Pinus coulteri D. Don (33,587 ha, Fig. 5).—A near endemic to California, Coulter pine is most widespread in the southern part of the state. It grows between 1000 and 2300 m on steep, concave slopes in association with dense chaparral and scrubby thickets of *Quercus chrysolepis* Liebm., mostly on windward escarpments (AAP, 40–100 cm). Coulter pine responds to stand-replacement burns with high colonizing ability and reproductive effort, with mass post-fire recruitment from seed release from partially serotinous cones, leading to even-aged stands (Borchert 1985; Vogl et al. 1988; Minnich 1999). Mixed-aged stands with arboreal subcanopy of *Q. chrysolepis* or *Q. kelloggii* Newb. occur on gentle slopes >1300 m (cf. Sawyer et al. 1988). Trees exhibit parallel decreasing cone serotiny with increasing elevation as stands shift from chaparral to oak woodlands (Borchert 1985). It is common in the northern Sierra Madre and San Rafael Mountains, and locally in the Santa Ynez Mountains. After a gap of 150 km, it recurs at Big Tujunga Canyon in the western San Gabriel Mountains and extends eastward into desert slopes at Rock Creek and coastal slopes to Crystal Lake. In the San Bernardino Mountains, Coulter pine is scattered across the southern escarpment east of Waterman Canyon. A continuous belt covers desert drainages from Lake Arrowhead to Holcomb Creek. It is extensive in the San Jacinto, Santa Ana, Hot Springs, Volcan, Palomar, and Cuyamaca Mountains but is not known from the Santa Rosa Mountains. The southernmost populations grow on Los Pinos Mountain. Stands tend to occur on granitic and sandstone substrates that weather into deep soils having secure moisture retention for post-fire recruitment. In drier ranges, where there is greater chance of reproductive failure from drought, Coulter pine frequently survives fire on bedrock slopes, similar to stands in Baja California (Minnich 1987). In spite of comparable climate and topography, Coulter pine does not occur in permeable Precambrian metamorphic gneisses and schists, including the Pelona Schist, that are extensively exposed in the Liebre, Frazier, and Alamo Mountains, as well as the eastern San Gabriel and western San Bernardino Mountains. It is also absent from extensive Eocene marine shales in Ventura County. Coulter pine sustained heavy mortality from insect predations during drought in 1989–1991. Mortality rates as high as 50 ha^{-1} were recorded in the San Jacinto Mountains (Savage

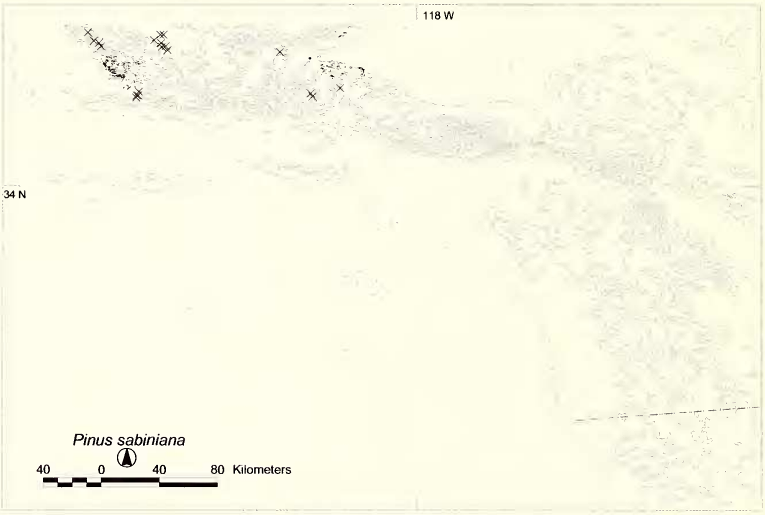

FIG. 6. The distribution of *Pinus sabiniana*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

1994). There were few changes in its range since the VTM survey.

Pinus torreyana Carrière (391 ha, Fig. 5).—The rarest pine in the world (Griffin and Critchfield 1976), Torrey pine occurs at only two localities near the ocean. One includes two stands spanning 6.0 km on rapidly eroding coastal bluffs incised into Eocene sandstone in San Diego Co.: a compact forest at Torrey Pines State Reserve and a fragmented population near Torrey Pines State Beach. The other locality is a 1.0 km forest growing in several ravines cut into upper Miocene sandstone above Beechers Bay on Santa Rosa Island, 270 km to the NW. Prescribed burn experiments shows that severe or fatal fire damage is followed by mass recruitment associated with seed dispersed from serotinous cones, similar to *P. coulteri* (Wells and Getis 1999). The low AAP of 25–35 cm at both localities is supplemented by fog drip (Schoenherr 1992) and is offset by low summer transpiration rates. Haller (1986) proposes that the island population be named *P. torreyana* ssp. *insularis* on the basis of gross morphology and garden plantings. Pollen grains in a sediment core taken from an estuary on Santa Rosa Island indicate that *P. torreyana* has been continuously present there since the middle Holocene (Cole and Liu 1994).

Foothill woodland. Foothill woodland consists of open parks of deciduous and evergreen oaks (*Quercus lobata* Nee, *Q. douglasii* Hook & Arn., *Q. agrifolia* Nee, *Q. wislizeni* A. DC.), scattered shrub cover, and exotic annual grassland (Griffin 1988). The California endemic *Pinus sabiniana* has an extensive range on foothill slopes encircling the Central Valley that are characterized by hot summers and an AAP of 30–60 cm.

Pinus sabiniana Douglas (3,931 ha, Fig. 6).—Gray pine grows in the San Rafael Mountains from Lazaro Canyon to Zaca Ridge. Colonies extend inland along Manzanita Creek and Sulphur Spring Canyon to Hurricane Deck where it grows on upper Cretaceous bedrock exposures. It is common in the Liebre Mountains. Botanical collections near Lake Piru mark the southern limit of the species. In the San Rafael Mountains, gray pine is found in mixed-aged stands, the trees apparently surviving understory fires. In the Liebre Mountains, many stands are even-aged due to stand-replacing chaparral burns, the recruitment establishing from seed released by serotinous cones. The distribution of gray pine is similar to that on VTM quadrangle maps.

Mixed evergreen forest. Mixed evergreen forest, which comprises long-lived evergreen coniferous and hardwood trees, is extensive in the coastal ranges of northern and central California (Sawyer et al. 1988). In southern California, this type consists of the *Pseudotsuga macrocarpa–Quercus chrysolepis* phase. One outpost of *P. menziesii* grows near Lompoc.

Pseudotsuga menziesii (Mirbel) Franco var. *menziesii* (4.2 ha, Fig. 7).—A single colony occurs in a moist canyon in the Purisima hills (Griffin 1964). It is surrounded by chaparral and *Pinus muricata* D. Don stands. This population receives abnormally low precipitation for the species (AAP, 40 cm), and apparently survives on cool summers and the high water table of the watercourse. The nearest stand lies 150 km NW in the Santa Lucia Mountains.

Pseudotsuga macrocarpa (Vasey) Mayr (22,232 ha, Fig. 7).—A southern California endemic, this long-lived tree (Bolton and Vogl 1969; McDonald and Littrell 1976; Haston and Michaelson 1994) has a fragmented distribution of compact groves in steep canyons, north-facing slopes, and cliff faces

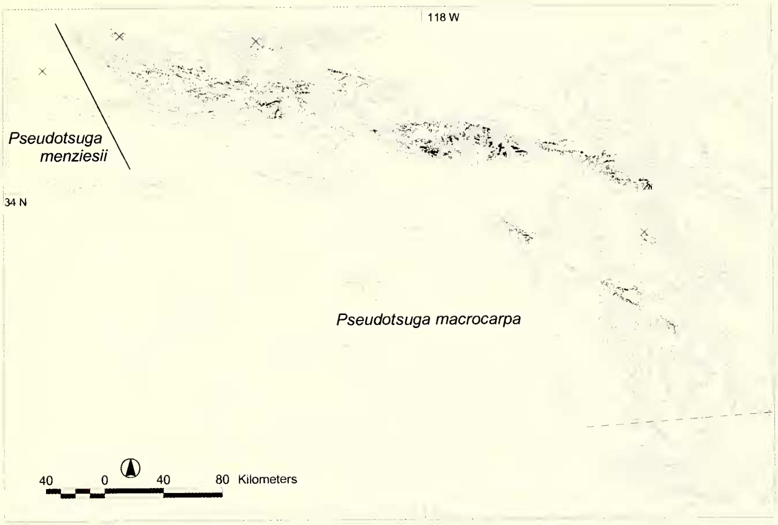

FIG. 7. The distribution of *Pseudotsuga macrocarpa* and *P. menziesii*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

between 1000 and 2200 m. Big-cone Douglas fir grows largely on windward escarpments, especially on slopes with high rates of erosion associated with fault-shattered substrate (AAP, 50–110 cm). The small-scale map in Griffin and Critchfield (1976) portrays a more continuous distribution than depicted on VTM quadrangle maps and Figure 7.

Rare colonies in La Brea Creek in the northern Sierra Madre Mountains are 20 km disjunct from abundant stands on Figueroa and Big Pine Mountains of the San Rafael Mountains. Numerous groves occur over an extensive area between the San Rafael Mountains and Lake Piru. Between Pine Mountain Ridge and Mount Pinos, big-cone Douglas fir is surprisingly abundant in semiarid badlands eroding into Quaternary alluvial terrace deposits and Pliocene sedimentary rocks, where it is associated with *Pinus monophylla* Torrey & Frémont. It is scarce on the undissected slopes of Mt. Pinos, Frazier Mountain, and Alamo Mountain, but common in canyons along the San Andreas fault in the San Emigdio and Liebre Mountains. Extraordinary stands grow at 600 m in the eastern Santa Susana Mountain badlands on Pliocene and upper Miocene marine sandstones and shales. Big-cone Douglas fir is extensively distributed in deeply incised canyons cutting into fault-shattered substrate of the San Gabriel Mountains. Continuous forests (stands >500 ha) are found near Mt. Wilson and Mt. San Antonio. In the San Bernardino Mountains, colonies span the southern escarpment and desert drainages west of Lake Arrowhead. In the Peninsular Ranges, big-cone Douglas fir is mostly restricted to escarpments of active faults. Along the Elsinore fault, it is common in the Santa Ana, Palomar, and Volcan Mountains. It is uncommon along the San Jacinto fault from Bautista Mountain to Thomas Mountain. *Pseudotsuga macrocarpa* is not known from the Santa Rosa, Hot Springs, Cuyamaca, and Laguna Mountains.

Although big-cone Douglas fir survives recurrent fire in association with arboreal *Quercus chrysolepis* in convex canyons, it has recently sustained widespread extirpations from wind-driven chaparral fires. In the eastern San Gabriel and San Bernardino Mountains, stand-replacement burns have exceeded recolonization rates, resulting in a net extirpation of 18% of forests since the 1938 aerial photographs (Minnich 1999). Current losses may be a natural perturbation due to variability in the fire process. However, fires should not act to synchronize stand age structure, nor produce extensive changes in the spatial extent of stands over short time scales because subcanopy burns result in continuous recruitment and high tree survivorship over multiple fire cycles. The extirpation of *P. macrocarpa* is not due to excess fuel build-up because regional fire intervals have changed little under fire suppression (Minnich and Chou 1997; Minnich 1999). Alternatively, the elimination of stands may be related to the nonrandomization of large fire occurrences to the severest weather conditions by suppression, notably Santa Ana winds (Minnich and Chou 1997). In the 19th century, forests were burned by low intensity fires persisting for months (Minnich 1987b). VTM stands have been reduced or extirpated in many areas of the Cobblestone and Topatopa Mountains, the eastern Transverse Ranges, Lake Hemet, Mt. Palomar, and Volcan Mountain.

Pinyon-juniper woodland. Pinyon-juniper woodland, which comprises *P. monophylla, Juniperus osteosperma* (Torrey) Little and *J. californica* Carrière, is widespread on leeward mountain slopes and along the margin of the Mojave and Sonoran Deserts. Trees grow with open shrub cover of Great

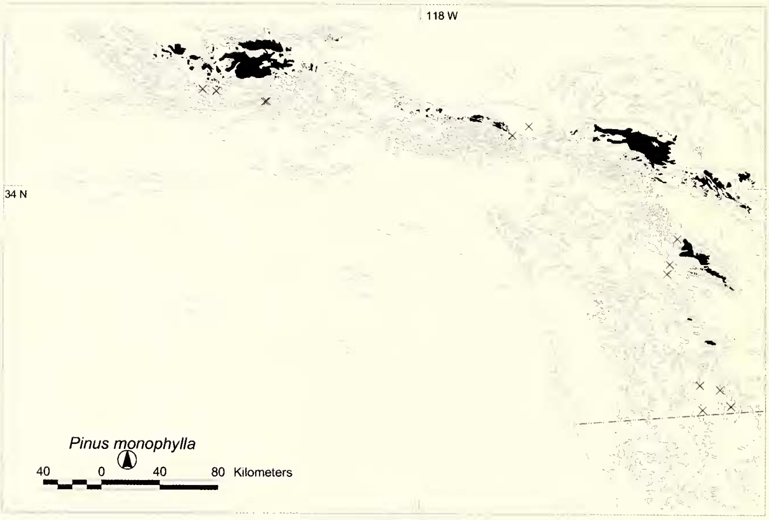

FIG. 8. The distribution of *Pinus monophylla*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

Basin sage scrub, desert chaparral, and Mojave Desert scrub. *Pinus quadrifolia* occurs in chaparral in inland coastal slopes.

Pinus monophylla Torrey & Frémont (156,815 ha, Fig. 8).—Single-leaf pinyon is found on leeward escarpments from 1300–2700 m (AAP, 20–50 cm). Extensive stands occur in the plateaus of the upper Cuyama River, Lockwood Valley, Sisquoc River, and Sespe Creek, including a few sandstone outcrops in the Topatopa Mountains. It is widespread on the northern escarpments of the San Gabriel and San Bernardino Mountains. A small population grows on fire-resistant cliffs in Cattle Canyon on the coastal slope of Mt. San Antonio (Thorne 1988). It is common in Joshua Tree National Park, especially on granites. In the Peninsular Ranges, *P. monophylla* is widespread only in the Santa Rosa Mountains from Pinyon Flat to Rabbit Peak. Small stands occur in the northeastern San Jacinto Mountains and the summits of Pinyon Ridge and Whale Peak. Outliers grow on Mt. Laguna and east of McCain Valley. Single-leaf pinyon is extensive above 1300 m in the northeast Mojave Desert. In the Colorado Desert, small stands cover two summits of the Eagle Mountains and another grows on the summit of the Coxcomb Mountains.

Based on needle resin duct morphology, it had been proposed that *P. monophylla* be divided into two varieties, *P. monophylla* var. *monophylla* in the northern Mojave Desert and *P. monophylla* var. *californiarum* in the Sierra Nevada and southern California, but *The Jepson Manual* does not recognize varieties of single-leaf pinyon (Lanner 1999).

Since the VTM survey, stand-replacement burns have removed single-leaf pinyon stands at Rock Creek and near Wrightwood in the San Gabriel Mountains, in the northern San Bernardino Mountains, Pinyon Flat in the Santa Rosa Mountains, and northwestern Joshua Tree National Park. However, the distribution of single-leaf pinyon appears to be stable because low primary productivity rates associated with low AAP limit fire intervals in the order of centuries, and gradual recolonization is seen in burns dating to the early 19th century (Wangler and Minnich 1996). Establishment does not appear to be limited by fire size due to efficient seed dispersal and caching by birds and rodents (VanderWall 1997).

Juniperus californica Carriére (149,464 ha, Fig. 9).—California juniper is common between 800 and 1700 m on alluvial bajadas extending onto the Mojave Desert from the Sierra Nevada and the north slope of Transverse Ranges to Joshua Tree National Park. It is locally abundant on the leeward flank of the Peninsular Ranges, with extensive stands in the Santa Rosa Mountains. Outposts occur in semiarid coastal drainages, including the Cuyama River, upper Soledad Canyon, alluvial fans of the Transverse Range (Azusa, Lytle Creek, Redlands), and in the Riverside-Perris Plain (Temescal Canyon, Lake Mathews, Gavilon Hills, Perris, Lakeview Mountains, Aguanga). A few trees occur near the coast in the Santa Monica Mountains (Raven and Thompson 1966) and in the Santa Ana Mountains. The AAP ranges from 20–40 cm.

Extensive stands mapped by VTM workers in the Mojave Desert have been denuded by fires carried by exotic grassland dominated by *Bromus madritensis* L. and *Schismus barbatis* L. (Lovich and Bainbridge 1999). Stands have also been cleared for development.

Juniperus osteosperma (Torrey) Little (1,619 ha, Fig. 10).—Utah juniper occurs in the eastern Transverse Ranges between 1500 and 2200 m (AAP, 20–35 cm). In the San Gabriel Mountains, a few stands grow near Phelan. It is common on the northern

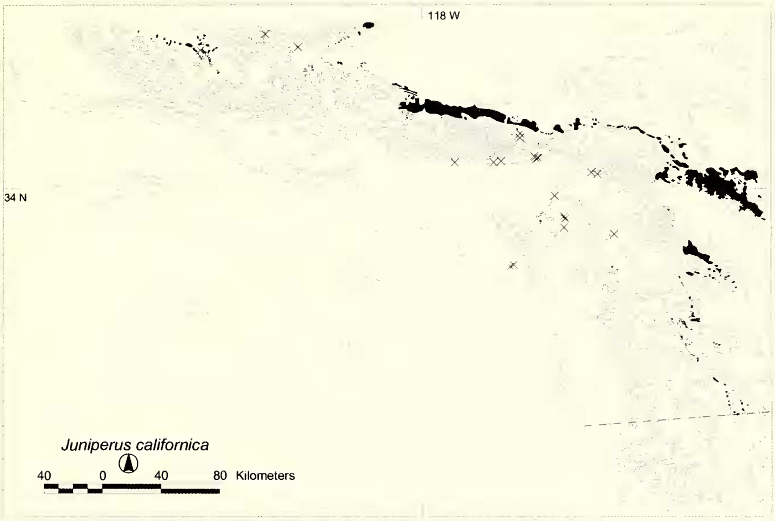

FIG. 9. The distribution of *Juniperus californica.* Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

escarpment of the San Bernardino Mountains from Grapevine canyon to Tip Top Mountain, with stands concentrating on carboniferous calcite and dolomite marbles. Large stands have been extirpated by the development of limestone quarries. Botanical collections of F. C. Vasek (UCR) indicate that most specimens are intergrades with *J. occidentalis* Hook. var. *australis* and *J. californica* Carrière. Utah juniper is common in the higher ranges of the northeast Mojave Desert.

Pinus quadrifolia Parl. (668 ha, Fig. 11).—An endemic to the Peninsular Ranges of southern California and northern Baja California, four-needle pinyon grows in chaparral from 1300–1800 m (AAP, 35–55 cm). The largest stands occur at Thomas Mountain, southern Garner Valley, and Vandeventer Flat in the southern San Jacinto Mountains. Small stands occur 55 km south on Mt. Laguna and in McCain Valley. Time-series aerial photographs in the Sierra San Pedro Mártir show that stand-replacement burns are followed by rapid recolonization in mature chaparral. Since the VTM survey, large populations have established in 80-yr old chaparral at the south end of Thomas Mountain. Pinyon pines are not known for cone serotiny, and recruitment appears to be dependent on seed cached by birds and mammals.

Lanner (1999) proposes that *P. quadrifolia* is a hybrid between *P. monophylla* and *P. juarezensis* (a five-needle pinyon). The designation is based on

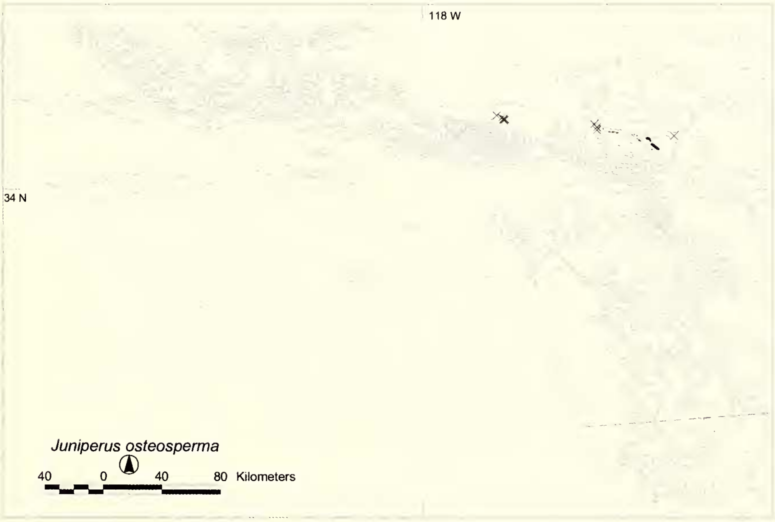

FIG. 10. The distribution of *Juniperus osteosperma.* Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

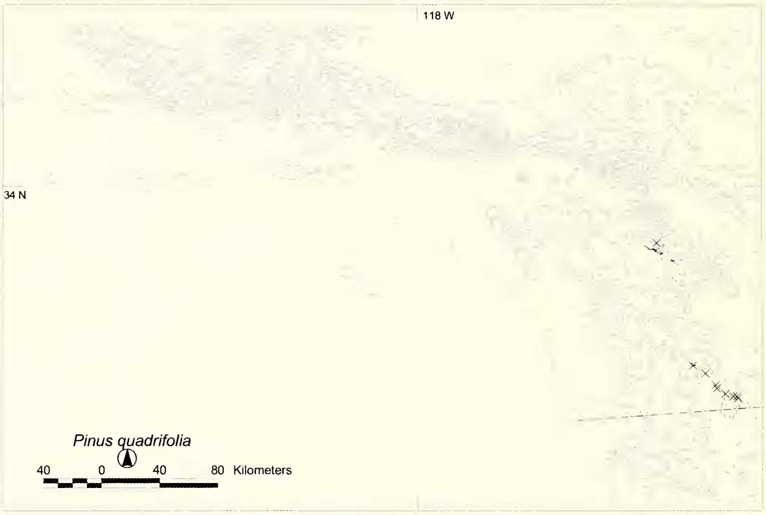

FIG. 11. The distribution of *Pinus quadrifolia*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

large variation in needle number, leaf resin canal number, twig hairiness and stomate position in populations of the La Rumerosa Plain near the Mexican border. However, *P. monophylla* and *P. quadrifolia* have strong ecologic and geographic segregation, with *P. monophylla* forming open stands on the desert-facing slopes and *P. quadrifolia* occurring in chaparral on coastal escarpments, their ranges broadly overlapping only on the La Rumerosa plain (Minnich 1987a). Monospecific *P. quadrifolia* woodlands, such as those on coastal slopes of the Sierra San Pedro Mártir or on Thomas Mountain, should be investigated for their morphological and genetic properties. *Pinus juarezensis* is not recognized in *The Jepson Manual* (Hickman 1993).

Mixed-conifer forest. While the modest elevations of the southern California mountains limit the spatial extent of mixed-conifer forest, the broad distribution of dominant tree species resembles those in the Sierra Nevada (Barbour and Minnich 2000). Mesic "westside" forests of *P. ponderosa, P. lambertiana, Calocedrus decurrens* and *Abies concolor* grow on windward slopes (AAP, 75–115 cm). Drier "eastside" forests of *P. jeffreyi, A. concolor* and *J. occidentalis* grow on leeward slopes (AAP, 30–75 cm). "Eastside" forests also cover thin soils on windward flanks of dissected ranges. Mixed-conifer forest grows in areas with low combustible shrub biomass, mostly at higher altitudes above the chaparral belt (>1500–2200 m) or in shrub-free basins within the chaparral belt (Minnich 2001). Subcanopy consists of open cover of montane chaparral dominated by *Arctostaphylos pringlei* C. Parry, *A. patula* E. Greene, *C. cordulatus* Kell., *Ceanothus integerrimus* Hook. & Arn., *Cercocarpus ledifolius* Nutt., *Chrysolepis sempervirens* (Kell.) Hjelmq., and *Rhamnus californica* Eschsch. Important hardwood associates are *Q. chrysolepis* and *Q. kelloggii.* Mixed-conifer forest is not found in the Santa Ana Mountains despite summit altitudes of 1700 m.

Pinus ponderosa Laws (22,841 ha, Fig. 12).—In southern California, VTM workers identified Jeffrey pine as *P. ponderosa* var. *jeffreyi,* resulting in ambiguous differentiation between *P. ponderosa* and *P. jeffreyi* (Griffin and Critchfield 1976). VTM maps show confusion in the Transverse Ranges where *P. ponderosa* was erroneously shown to be extensive. In our survey, ponderosa pine was distinguished from Jeffrey pine on aerial photographs based on deeper yellow-green (blue-green) foliage and more cylindrical (conical) shape of canopies of ponderosa (Jeffrey) pine. In the field we noted for foliage color and yellow (brown) immature cones of ponderosa (Jeffrey) pine. The reduction in the spatial extent of ponderosa pine in Fig. 12 compared to VTM maps is consistent with its decreasing importance southward in California.

Ponderosa pine is most abundant in areas with high AAP and deep soils between 1400 and 2100 m. Small colonies cover the San Rafael Mountains, and it is common along Pine Mountain Ridge. Ponderosa pine appears to be absent from Mt. Pinos, Frazier Mountain, and Alamo Mountain (Vogl and Miller 1968). We saw a few stems on groundwater seeps along the San Andreas fault in Cuddy Valley and north of Mt. Pinos. A monotypic stand covers Sawmill Mountain in the Liebre Mountains. Ponderosa pine covers small basins or gentle summits in the San Gabriel Mountains. The largest stands grow from Mt. Waterman to Mt. Islip and near Crystal Lake (cf. Thorne 1988). The only extensive stand is a 30-km belt along an old erosion surface of weathered granite in the western San Bernardino Mountains. Trees grow as low as 1100 m, compa-

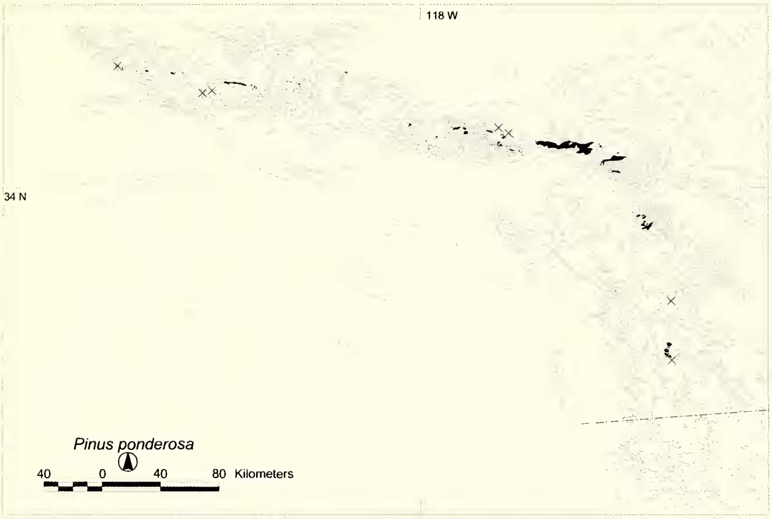

FIG. 12. The distribution of *Pinus ponderosa*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

rable to other "westside" stands in the Sierra Nevada. Large stands grow at Barton Flats and Mill Creek. In the Peninsular Ranges, ponderosa pine occurs on the west flank of Mt. San Jacinto. To the south, a small colony grows at Doone Valley on Mt. Palomar, and a single tree 30 m tall straddles an arroyo on Hot Springs Mountain at 1600 m. Stands on Mt. Cuyamaca represent the southern limit of the species along the Pacific Coast.

Calocedrus decurrens (Torrey) Florin (13,952 ha, Fig. 13).—The range of incense cedar is similar to *P. ponderosa,* except that it concentrates on stream courses from 1100 to 2200 m. It occurs locally in the San Rafael Range and in one north-facing canyon of the northern Sierra Madre. Stands are common from Pine Mountain Ridge to Alamo Mountain, and from the San Emigdio Mountains to the Tehachapi Mountains. It grows in canyons throughout the San Gabriel Mountains. In the San Bernardino Mountains, incense cedar forms widespread understory thickets in dense ponderosa pine forest from Crestline to Running Springs, in Barton Flats, and in Mill Creek, with stands concentrating near watercourses in open forests (Minnich et al. 1995). Subcanopy thickets are also widespread in the northern San Jacinto, Palomar, and Cuyamaca Mountains. Local mature stands grow in the drier Santa Rosa, Hot Springs, Volcan, and Laguna Mountains.

Pinus lambertiana Douglas (53,477 ha, Fig.

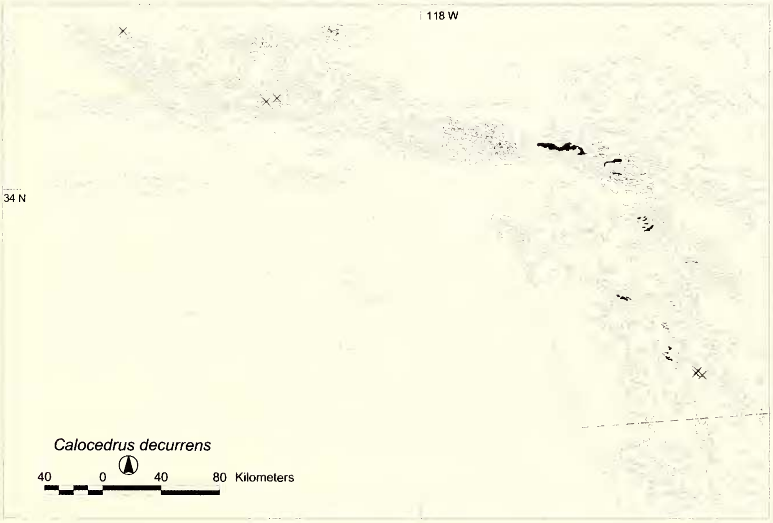

FIG. 13. The distribution of *Calocedrus decurrens*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

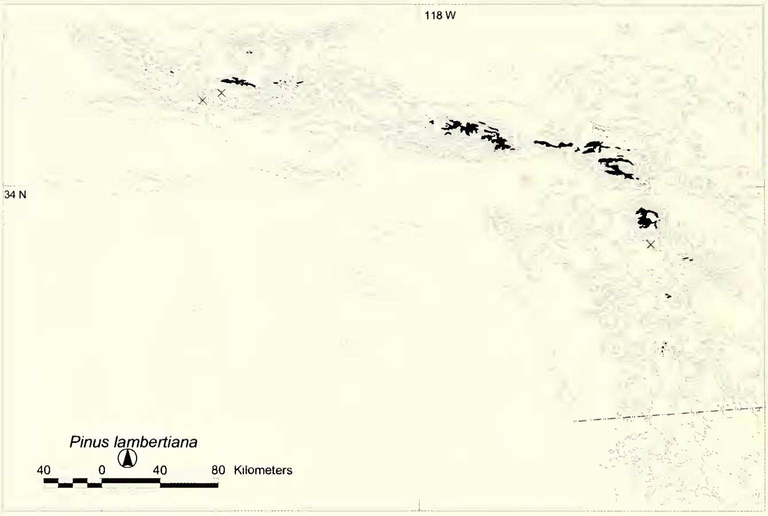

FIG. 14. The distribution of *Pinus lambertiana.* Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

14).—Sugar pine is common on steep, mostly north-facing slopes between 1700 and 2700 m. Isolated colonies grow in the San Rafael Mountains, but it is extensive on Pine Mountain Ridge, Cobblestone Mountain, and north-facing cliffs of the Topatopa Mountains. It is rare in the semiarid ranges to the north, except locally on Mt. Pinos. Sugar pine is common across the San Gabriel and San Bernardino Mountains, but is absent on leeward slopes near Wrightwood and Big Bear. In the Peninsular Ranges, it is widespread only on Mt. San Jacinto. Local stands grow on the Santa Rosa, Hot Springs, and Cuyamaca Mountains. It is not known from the Palomar, Volcan, and Laguna Mountains.

Abies concolor (Gordon & Glend.) Lindley (107,415 ha, Fig. 15).—Vasek (1985) provides evidence that southern California white fir is the Rocky Mountain variety *A. concolor* var. *concolor,* whereas the Pacific coast variety *A. concolor* var. *lowenia* grows in the Sierra Nevada southward to the Tehachapi Mountains. White fir is often dominant on north-facing slopes from 1500 to 2800 m. It grows in the San Rafael Mountains, along Pine Mountain Ridge, and in "eastside" forests covering the Mt. Pinos, San Emigdio, Alamo, Frazier, and Tehachapi Mountains. White fir is found throughout the San Gabriel and San Bernardino Mountains with extensive subcanopy thickets growing in the dense mixed-conifer forests at Lake Arrowhead and Barton Flats (Minnich et al. 1995). The tree is

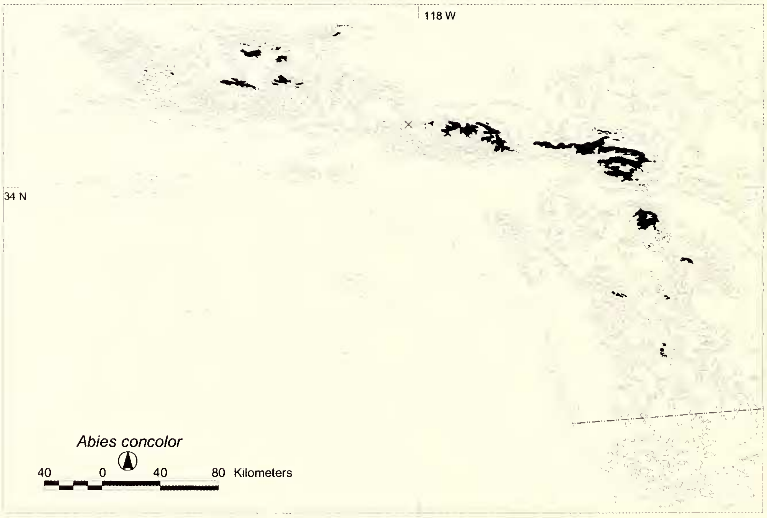

FIG. 15. The distribution of *Abies concolor.* Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

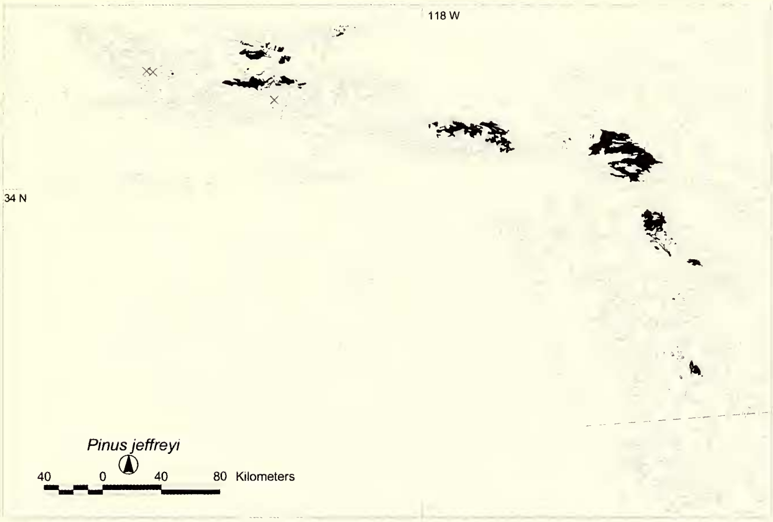

FIG. 16. The distribution of *Pinus jeffreyi*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

widespread on Mt. San Jacinto, and an invasive subcanopy tree near Idyllwild. Small populations occur on Palm Divide, Santa Rosa Mountain, Thomas Mountain, and Hot Springs Mountain. White fir is invasive in the Palomar and Cuyamaca Mountains. A VTM record of white fir in the Volcan Mountains cannot be confirmed, and it is not known from the Laguna Mountains. The Rocky Mountain variety grows in the Kingston and Clark Mountains of the northeast Mojave Desert.

Pinus jeffreyi Grev. & Balf. (124,551 ha, Fig. 16).—Jeffrey pine is the forest dominant >2000 m in southern California. It also covers local shrub-free basins in the chaparral belt to as low as 1100 m in monospecific stands. Jeffrey pine typically replaces *P. ponderosa* along decreasing precipitation gradients. The confusion of *P. jeffreyi* and *P. ponderosa* by VTM workers resulted in maps erroneously showing *P. jeffreyi* in areas where only *P. ponderosa* occurs.

Jeffrey pine is extensive on Pine Mountain Ridge, Mt. Pinos, Frazier Mountain, Alamo Mountain, and the San Emigdio Mountains. Monotypic stands extend downslope into Lockwood Valley and along the Cuyuma River plain to 1300 m. A few trees grow in the San Rafael Mountains. It spans the San Gabriel Mountains and the San Bernardino Mountains east of Lake Arrowhead. Jeffrey pine is common on Mt. San Jacinto, Santa Rosa Mountain, and the summit of Thomas Mountain. It is extensive in nearby Garner Valley at 1400 m, and a large VTM stand to the east was mistaken for *P. coulteri.* A single stand grows on Hot Springs Mountain (it was shown as *P. ponderosa* on VTM maps), but a few trees near Palomar Mountain Observatory appear to be planted. Jeffrey pine is common in the Cuyamaca Mountains and forms monotypic stands on the Laguna Mountain plateau and adjoining basins. The southernmost population is at Pine Valley at an altitude of 1100 m.

Juniperus occidentalis Hook. var. australis (Vasek) A. Holmgren & N. Holmgren (23,011 ha, Fig. 17).—Sierra Nevada western juniper is found locally on Wright Mountain, Mt. San Antonio, and in Icehouse Canyon in the eastern San Gabriel Mountains. In the San Bernardino Mountains, it is widespread with Jeffrey pine >2100 m on the semiarid plateaus near Big Bear, with stands frequently extending into pinyon-juniper woodland. Ancient trees with dbh >2–3 m are seen from Sugarloaf Mountain to Onyx Summit. Isolated trees occur on San Gorgonio Mountain, the southern limit of the species.

While members of mixed conifer forest exhibit extensive range overlap, species boundaries are invariably congruent at the edge of recent stand-replacement burns. Congruent boundaries also occur at the chaparral ecotone. These trends reflect the similar adaptations of these conifers (tall stature, thick bark) to survive subcanopy burns recurring 2–3 times per century (Minnich et al. 2000). All mixed-conifers are selectively eliminated by stand-replacement fires in chaparral. Since the VTM survey, fire suppression has led increasing fire intervals and stand-densification, with an age-specific trend away from dominance by *P. ponderosa* or *P. jeffreyi,* and toward dominance by juvenile, pole-size classes of *A. concolor* and *C. decurrens* (Ansley and Battles 1998; Minnich 1988; Minnich et al. 1995; Roy and Vankat 1999; Minnich et al. 2000). Increasing fuel loads and stand-densification have led to widespread stand-replacement burns (Minnich 1999; Barbour and Minnich 2000; Minnich et al. 2000), similar to that in the Sierra Nevada (Weatherspoon et al. 1992; McKelvey and Johnston 1992; SNEP 1996). Stands that were

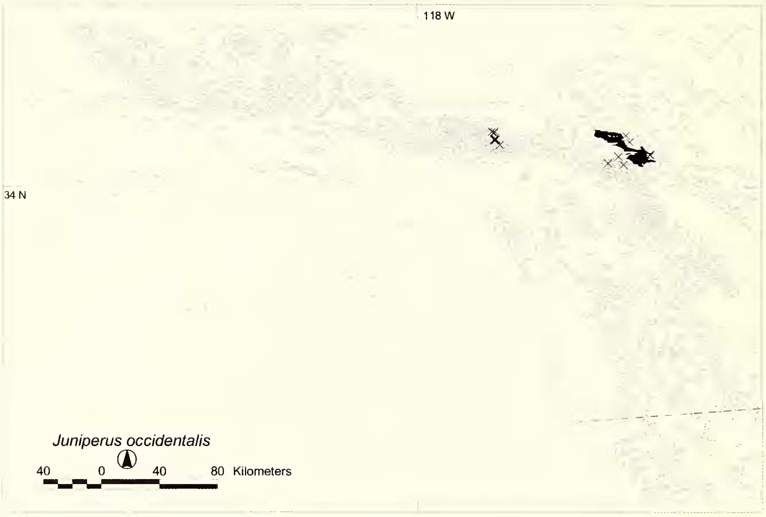

FIG. 17. The distribution of *Juniperus occidentalis*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

logged during the late 19th century, mostly at Lake Arrowhead, Idyllwild, Mt. Laguna and Mt. Cuyamaca (Minnich 1988; Pryde 1984) have densities exceeding 300–500 stems ha^{-1}, or are 1.5 to 6 times that recorded in forests sampled by VTM workers in 1929–1934, and in the Sierra San Pedro Mártir, Mexico, where open parklike forests are produced by intense subcanopy burns at intervals of 50 years without fire control (Minnich et al. 1995, 2000). In southern California, open forests persist on drier leeward slopes with low primary productivity (Minnich et al. 1995) or in steep, dissected ranges with thin soils such as the San Gabriel Mountains. Crown fires have denuded extensive stands (>500 ha units) mapped by VTM workers, with stands being replaced by successional montane shrublands, *Q. chrysolepis* and *Q. kelloggii* (cf. Kauffman and Martin 1990, 1991). Portions of VTM forests were extirpated at Pine Mountain Ridge, Alamo Mountain, Frazier Mountain, as well as Pleasant View Ridge, Prairie Fork, Ontario Peak, and Cucamonga Peak in the San Gabriel Mountains. Extirpations also occurred near Big Bear Lake and Raywood Flat in the San Bernardino Mountains, Mount San Jacinto, Mount Cuyamaca, and the south edge of the Laguna Mountain plateau.

Subalpine forest. Subalpine forest grows on isolated summits >2500 m (AAP, 40–100 cm). Compared to the Sierra Nevada, southern California subalpine forests are floristically depauperate, with only two pine species occurring in the region.

Pinus contorta Loudon ssp. *murrayana* (Grev. & Balf.) Critchf. (11,696 ha, Fig. 18).—In the San Gabriel Mountains, lodgepole pine occurs from Throop Peak to Mt. Baden-Powell, and on summits from Mt. San Antonio to Cucamonga Peak. In the San Bernardino Mountains, it grows on slopes and valley floors at Butler Peak, Sugarloaf Mountain, Holcomb Valley, Bluff Lake, Big Bear, and the upper Santa Ana River. It dominates subalpine forests on San Gorgonio Mountain. The southernmost stands occur on Mt. San Jacinto and Tahquitz Peak.

Pinus flexilis James (6,642 ha, Fig. 19).—Small colonies grow on Mt. Pinos and nearby Cerro Nordeste. In the San Gabriel Mountains, the only major population extends from Throop Peak to Mt. Baden-Powell; a few trees occur 10 km E on Wright Mountain. It is strangely absent from lodgepole pine forests near Mt. San Antonio. In the San Bernardino Mountains, limber pine is common on Sugarloaf Mountain, Onyx Summit, and other semiarid peaks in the upper Santa Ana River where it grows with "eastside" stands of *P. jeffreyi*, *A. concolor*, and *J. occidentalis*. At Onyx Summit (AAP, 35 cm), limber pine forms ecotones with single-leaf pinyon woodlands, similar to forest zonation in the Great Basin. It is common >2,800 m on Mt. San Gorgonio. In the San Jacinto Mountains, stands grow on Mt. San Jacinto and Tahquitz Peak. Maps of Griffin and Critchfield (1976) show them 15 km too far east. A small population on Toro Peak in the Santa Rosa Mountains is the southern limit of the species.

While subalpine forests in southern California experience numerous small burns initiated by lightning, site-specific mean fire intervals are in the order of centuries (Sheppard and Lassoie 1998). Stands show local patchiness from 19th century stand-replacement burns on the San Bernardino Ridge, Mt. Grinnell (Minnich 1988), and the east face of Mt. San Jacinto. Since the VTM survey, stand-replacement burns have occurred in the upper Whitewater River near Mount San Gorgonio, near Butler Peak, and on Ontario Peak. All burns are regenerating well.

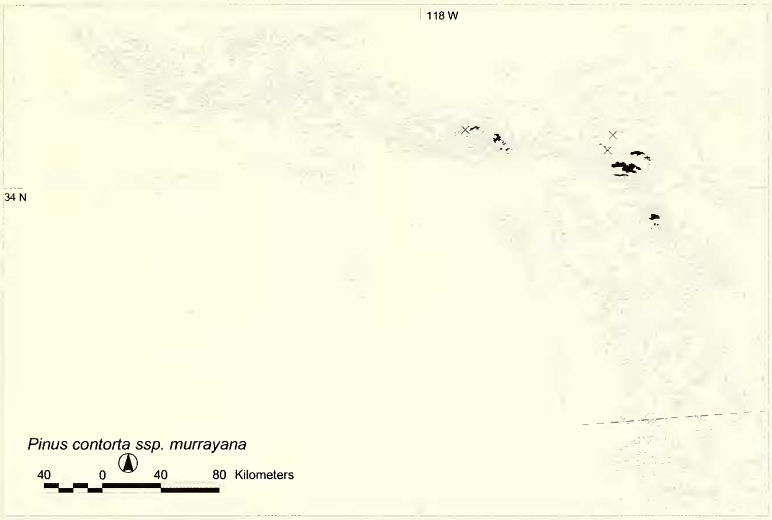

FIG. 18. The distribution of *Pinus contorta*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

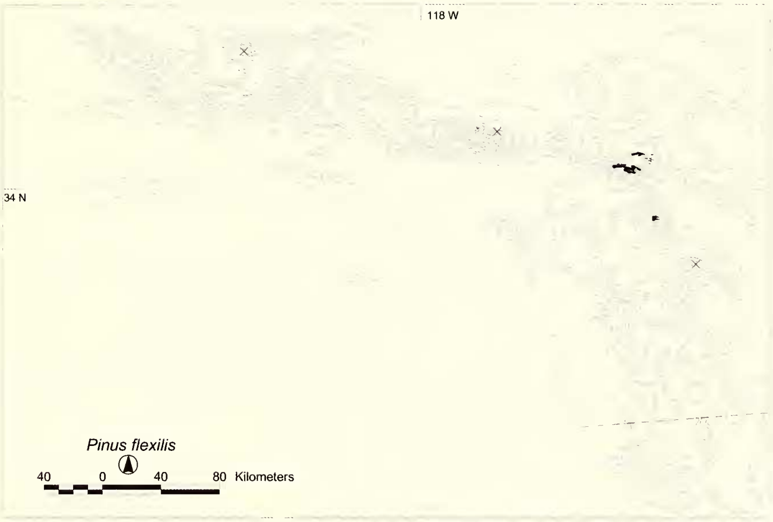

FIG. 19. The distribution of *Pinus flexilis*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

DISCUSSION

While distributions viewed statically provide insight into ecological relationships, how a species adapts to an environment can also be evaluated from a synoptic time-series frame of reference. In addition, a regional approach permits the examination of the broadscale status of populations as seen in time- and space-averaging of local scale population dynamics. The assessment of stand dynamics is not straightforward with respect to whether species changes reflect normal biomass removal and accumulations from fire and postfire successions, or whether they reflect long-term directional change. This distinction cannot be made here from a time-series comparison of forest maps only 70 years apart. However, for the purpose of hypothesis testing of population stability, we propose that vegetation baselines in southern California be interpreted using three fire disturbance models which address key processes or patterns that influence stability.

Shifting population model (closed-cone conifer forests, Pinus quadrifolia *woodland).* The large size of chaparral stand-replacement burns (two to three per century) relative to the size of individual conifer populations tends to synchronize stand age distributions across entire stream drainages, resulting in large temporal variation in their spatial extent at local scales. Stands "disappear" in recent burns, but emerge as even-aged stands in older chaparral patches, "following" old-growth patch mosaics. To evaluate the stability of shifting populations, it may be best to search for postfire recruitment failures (stands which fail to reestablish after burns, e.g., Zedler 1981; Vogl et al. 1988) because individual fires can eliminate both the adult population and the seed bank, resulting in local extinctions. *Pinus quadrifolia* forests have these characteristics, but individual stands are mixed-aged because recruitment is continuous through successions.

Standing population model (mixed-conifer forest, mixed-evergreen big-cone Douglas fir forest, gray pine foothill woodland). The canopy layer persists through recurrent subcanopy fires (two to three per century), resulting in "standing" or fixed distributions with small local fluctuations. Although trees recruit continuously, stands undergo intense selective elimination of sapling and polesize trees from subcanopy fires, with a few mid-size trees incrementally joining the canopy layer between fire sequences, producing mixed-aged overstory. Discrete age mosaics in the canopy layer are rare because stand-replacement burns are rare. Stands occupy sites safe from dense shrub subcanopy that normally produce stand-replacement fires, especially chaparral. Stability can be evaluated from the long-term expansion or contraction of "standing" tree populations over multiple fire cycles. A key factor may be the spatial extent of individual stand-replacement burns, and whether stand attrition is balanced by recolonization. Since the initiation of fire suppression, stand-replacement burns have frequently exceeded 1000 ha, whereas patches created by crown fires rarely exceed 10 ha without fire control in mixed-conifer forests of the Sierra San Pedro Mártir of Baja California (Minnich 1999; Minnich et al. 2000).

Patch mosaic population model (pinyon-juniper woodland, subalpine forest). Low productivity rates and stand structure result in long interval subcanopy to canopy fires (return intervals <1 per century). Stand mortality is high because the flame front both consumes tree canopy, and the thin bark of partially burned conifers results in fatal cambium damage. Stands exhibit discrete inter-stand age structures arrayed in a patch mosaic. Individual stands are mixed-aged due to continuous recruitment, especially in shade-tolerant species such as *P. monophylla* and *P. flexilis.* Trees exhibit little change in broadscale distributions, but patches appear in the form of recent stand-replacement burns. These patches fade after 50–100 years as recruitment gradually establishes closed canopy. Older age class boundaries are subtle because fire return intervals scale at several per millennia. Trees are longer-lived than members of closed-cone conifer forests and stability is harder to establish over time scales of a century. The potential for destabilization of forests may again be reflected in the size of stand-replacement burns.

How can these population models be applied to long-term species changes? While the distribution of conifer forests has been altered by fire over the past century, the stability of these ecosystems cannot be judged alone by the historical severity and spatial extent of fires. Fire regimes in California forests are an outgrowth of cumulative fuel build-up scaling from several decades to centuries, the time lag between fuel accumulation and burning making fire self-limiting, and time-dependent (Minnich and Chou 1997; Minnich et al. 2000). The site-specific properties of fire (intervals, intensities, removal of biomass) vary with climate, primary productivity, and fuel accumulation rates and exert profound selection in tree species distributions depending on their life history traits (Veblen et al. 1991; Christensen 1993; Johnson and Gutsell 1994). Forest ecosystems tend to burn most frequently in areas with highest productivity (cf. Knight 1987; Veblen et al. 1991). In southern California growth rates are proportional to mean annual rainfall, except at highest elevations (>ca. 2300 m) where productivity is limited by short growing seasons. Fire return intervals range from two to three times per century in closed-cone, mixed-evergreen, and mixed-conifer forest on moist coastal windward slopes (Minnich and Chou 1997; Minnich et al. 2000) to <1 per century in pinyon-juniper woodland on semiarid leeward slopes (Wangler and Minnich 1996) and subalpine forests on highest summits. Fire severity and conifer mortality rates also vary because conifer species are associated with divergent subcanopy vegetation and vertical distribution of fuels (Minnich 2001).

The role of climate variability on fire regimes and long-term directional change of forests is a gradual process because fire outcomes are an outgrowth of long-term vegetation successions and fuel build-up. Directional vegetation changes also lag behind climatic perturbations because selection processes that result in changes in recruitment and successions require several generations to translate into mature phases of the vegetation.

Fire suppression, which is unprecedented in ecological history, may produce rapid change, especially where fires have been excluded from forests for extended periods. In addition, the intensity of large fires may have increased because suppression both encourages excessive fuel build-up where fire intervals have lengthened and selectively restricts uncontrolled fires to the severest weather conditions (Minnich and Chou 1997). Forests experiencing shifting or patch mosaic population dynamics normally experience high fire severity and mortality, and how changes in fire intensity with suppression would change the stand-replacing fire regime is unclear. Fire intervals in chaparral and closed-conifer forests have been stable with or without suppression (Minnich and Chou 1997). Unproductive patch mosaic model ecosystems may be well within presuppression fire-free periods. In spite of local removal of forests by stand-replacement burns, the spatial extent of conifer species having shifting and patch mosaic population dynamics has changed little during the 20th century. The demonstration of long-term change in these ecosystems would require evidence that replacement recruitment rates are dependent on the survivorship of the adult population. Reduced reproductive potential in short interval fire recurrences may be infrequent because the turnover of patch mosaics is dependent on cumulative fuel build-up. Invasive exotic annual grasses that produce abundant cured fuel, including *Bromus madritensis* L., *B. diandrus* Roth, and *Avena barbata* Link, may increase the frequency of short-interval burn sequences and degradation of coastal sage scrub and chaparral (Freudenberger et al. 1987; Minnich and Dezzani 1998). However, invasive species are generally limited to coastal valleys and lower foothills far removed from conifer ecosystems. Directional change in closed-cone conifers may arise from post-fire recruitment failure due to short-term extreme environmental conditions, such as drought, but on the basis of chance extreme conditions seldom coincide with fire cycles over long time scales.

Recent fire history suggests that the greatest potential for directional vegetation change may occur in ecosystems having "standing" population dynamics due to increasing fire severity and stand mortality (Minnich 2001). The maintenance of standing forests (mixed-conifer forest, bigcone Douglas fir forest) with recurrent subcanopy fires may be compromised by increasing fire intervals (e.g., Swetnam 1993; Minnich et al. 2000), stand-densification (Minnich et al. 1995; Albright 1998; Roy and Vankat 1999) and increasingly extensive stand-replacement burns. Over long time scales, the transformation of these forests from "standing" population dynamics to either "shifting" or "patch mosaic" dynamics may result in progressive regional extirpations, a trend seen in the 20th century.

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